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低海拔和高海拔产区气象因子对‘美乐’葡萄浆果品质和代谢组的影响*

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摘 要 为明确低海拔(41 m)和高海拔(2 343 m)‘美乐’葡萄产区浆果代谢组和品质的差异和成因，试验采用GPRS-Base系统气象站监测低海拔和高海拔‘美乐’葡萄产区的气象因子，采用气相色谱/飞行时间质谱(GC/TOF-MS)技术解析低海拔和高海拔产区‘美乐’浆果代谢组的差异，并测定了不同海拔‘美乐’葡萄浆果的可溶性固形物含量、pH、总酸含量、还原糖、花青素、总酚、单宁、黄酮、类黄酮和蛋白质的含量。结果表明，高海拔‘美乐’葡萄产区平均日照时数、生育期总辐射、日均辐射、日均温差、日均温度、生长时期有效积温等气象因子均高于低海拔‘美乐’葡萄产区；与低海拔产区相比，高海拔产区的‘美乐’葡萄浆果的可溶性固形物、单宁和还原糖含量增加，总酚和花青素含量减少。代谢通路分析表明：高海拔产区的葡萄浆果积累更多的氨基酸、有机酸、醇、多酚、糖类等物质。代谢通路富集表明：高海拔产区改变了葡萄浆果 8 条氨基酸代谢、4 条碳水化合物、3 条脂质代谢和 3 条氮代谢通路。去趋势化对应分析表明：‘美乐’葡萄园中的气象因子如日均日照时数、生长时期总辐射、日均辐射、温差、日均温度、生长时期有效积温是驱动‘美乐’浆果代谢物积累的主要因子。高海拔和低海拔区域气象因子的差异是‘美乐’葡萄浆果代谢物差异的重要驱动力，高海拔区‘美乐’葡萄浆果通过代谢物和代谢通路的多样性策略来适应高海拔环境，提高浆果的品质。

关键词 ‘美乐’葡萄浆果 海拔梯度 代谢物 代谢组学 气象因子 代谢通路 通路富集
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Response of ‘Merlot’ grape berry quality and metabolome to meteorological factors at both low and high altitudes*

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Abstract To illustrate the adaptability and quality characteristics of ‘Merlot’ grape berries in high altitude production areas, the metabolites contents and metabolomics of ‘Merlot’ grape berries were analyzed in relation to meteorological factors at low (41 m) and high (2 343 m) altitude wine-producing areas. In this investigation, meteorological factors at low/high-altitude of wine-producing areas were monitored by GPRS-based system. The pH and contents of soluble solids, total acid content, reducing sugars, anthocyanin, total phenol, tannin, flavonoid, flavone and proteins of ‘Merlot’ grape berries were determined. Furthermore, GC/TOF-MS technique was used to analyze the difference in metabolome of ‘Merlot’ grape berries between

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different altitudes. The results showed that average daily sunshine duration, total radiation during grapes growth period, average daily radiation, average daily temperature difference, average daily temperature and effective cumulative temperature during growth period were higher in high-altitude than those in low-altitude regions. The contents of soluble solid, tannin and reducing sugars of ‘Merlot’ grape berries increased, while the contents of total phenols and anthocyanin decreased in high-altitude wine-producing area, compared with those in low-altitude wine-producing area. Metabolic pathway analysis indicated that ‘Merlot’ grape berries in high-altitude wine-producing area accumulated more amino acids, organic acids, alcohols, polyphenols and sugars than those in low-altitude wine-producing area. Metabolic pathway enrichment analysis showed that 8 amino acid metabolome pathways, 4 carbohydrate metabolome pathways, 3 lipid metabolome pathways and 3 nitrogen metabolome pathways of ‘Merlot’ grape berries were regulated in high-altitude region. DCCA (Detrended Canonical Correspondence Analysis) indicated that average daily sunshine duration, total radiation, average daily radiation, average daily temperature difference, average daily temperature and effective cumulative temperature during growth period were the driving factors of ‘Merlot’ berries quality and metabolites. In conclusion, climatic factors were the main driving factors inducing metabolite differences between ‘Merlot’ grapes berries growing in low- and high-altitude regions. Thus, to adjust metabolites profiles and metabolic pathways was a kind of strategies of ‘Merlot’ grapes for adapting to high altitude ecological environments.
Keywords　‘Merlot’ grape berry; Altitude gradient; Metabolite; Metabolome; Climatic factor; Metabolic pathway; Pathway enrichment

‘美乐’葡萄(*Vitis vinifera* L. cv. Merlot)，又称‘梅洛’、‘梅鹿辄’，全世界总种植面积超过 260 000 hm^2 (OIV)，是世界三大红葡萄品种之一，是最开始用于酿制圣埃美隆(Saint-Emilion)及波美侯(Pomerol)佳酿的红葡萄品种，在全世界葡萄酒产区都有大面积种植。‘美乐’葡萄抗逆性好、早熟并且具有丰富的果味，在较反常的气候条件下，也能正常发育成熟，酿造时常与其他品种混酿[1–5]。研究认为风土(Terroir)如土壤、地貌、海拔、坡度、坡向和栽培管理等是影响葡萄浆果代谢物种类和含量的重要原因[6–8]，代谢物如氨基酸、有机酸、高级醇、酚类和糖类是葡萄适应环境的产物，这些代谢物参与多条代谢通路的调控，是人类重要的营养物质[1,5,9–18]。其中，海拔梯度是影响酿酒葡萄品质和代谢组的主要限制因子之一，近年来，‘美乐’在中国葡萄酒产区被广泛种植，如华东烟台、河北昌黎、西北贺兰山东麓(海拔 0~1 400 m)，在西南高原攀西地区(海拔 1 200 m)、云南弥勒(海拔 1 500 m)、云南高海拔区域干冷河谷区德钦县(海拔 2 343 m)和四川省小金县(海拔 2 500 m)都有种植。然而，对于高海拔区域‘美乐’浆果的品质和代谢物的积累规律缺少研究，因此有必要对低海拔和高海拔区域浆果的代谢物进行定量或定性研究。

近年来，代谢组学技术用于研究生物体对环境的响应[19]，为解释高海拔区域和低海拔区域葡萄代谢物和品质的差异提供了有效的分析技术。本研究应用气相色谱/飞行时间质谱(GC/TOF-MS)技术[20]解析‘美乐’葡萄浆果在高海拔区域(2 343 m)和低海拔区域(41 m)代谢组学的差异，紫外分光法普遍应用于葡萄品质和葡萄酒品质的分析[21–22]，研究中测定了‘美乐’浆果内含物含量，如可溶性固形物、pH、总酸、还原糖、花青素、总酚、单宁、黄酮和类黄酮含量等指标评价美乐浆果的品质。利用 IPA(整合的代谢通路分析)研究高海拔和低海拔葡萄浆果代谢通路的差异，MEPA(代谢通路富集)研究高海拔和低海拔葡萄浆果代谢通路富集，DCCA(去趋势化对应分析)方法进行葡萄浆果代谢物与高海拔和低海拔‘美乐’浆果葡萄园气象因子的关联分析[23–25]，以期从代谢组学的角度解释‘美乐’葡萄对高海拔环境的适应性和品质特征，了解高海拔区域‘美乐’葡萄品质的成因，为高海拔区域‘美乐’葡萄和葡萄酒的生产提供理论基础。

1　材料与方法

1.1　试验地点

2013—2014 年连续两年选择海拔 41 m 和 2 343 m 的 2 个‘美乐’葡萄园用于试验研究(表 1)，葡萄树龄均为 6 年。海拔 2 343 m 的葡萄园属低纬度高海拔产区，澜沧江河谷，阴坡，坡度 10°~30°，离澜沧江河面海拔落差 500 m。海拔 41 m 的葡萄园属于北回归线以北低海拔产区，平原，离渤海/黄海交界处 10 km，该产区是中国葡萄酒经典产区，近现代中国葡萄酒的起源地。

表 1　不同海拔梯度葡萄园试验点信息

Table 1　Informations of wineyards in wine-producing areas at different altitudes

葡萄产区 Wine-producing area	土壤类型 Soil type	海拔 Altitude (m)	经纬度 Latitude and longitude
山东省蓬莱市刘家沟 Liujiagou Village, Penglai City, Shandong Province	黄色海沙壤 Yellow sandy soil	41	37°11.00′N, 120°53.00′E
云南省德钦县九龙顶村 Jiulongding Village Deqing County, Yunnan Province	棕色沙砾土 Brown sandy soil	2 343	28°17′N, 98°52′E

1.2 气象数据监测

试验采用 GPRS-Base 系统气象站采集上述 2 海拔梯度葡萄园的气象数据，参照农业气象监测标准，连续两年监测大气环境中光辐射、温度、降雨量及相对湿度，每 15 min 记录一次数据。

1.3 浆果样品采集及后续处理

每个葡萄园随机选择 60 株、每株留枝量控制在 16 个结果枝的葡萄作为采样植株，采收花后 120 d 的 2 kg 成熟果粒。1 kg 成熟果粒 4 ℃保存，带回实验室做后续处理，方法参照文献[21]，处理好的样品储存在–20 ℃备用，用于测定可溶性固形物含量、pH、总酸含量、还原糖、花青素、总酚、单宁、黄酮、类黄酮和可溶性蛋白质含量；1 kg 成熟果粒随机混合后分装在 18 个 50 mL 的离心管中，–80 ℃液氮保存，用于代谢组学分析。

1.4 浆果品质分析

利用温度补偿数字折射仪(Antago, PAL-1,日本)测定浆果的可溶性固形物含量，测定温度控制在 25 ℃，具体方法参照文献[21]。利用 Ti-touch(瑞士，万通)测定浆果的 pH 和总酸含量，pH 8.2 作为滴定终点(OIV，1990)，总酸含量表示为 $g{\cdot}L^{-1}$。还原糖、花青素、总酚、单宁、黄酮和类黄酮含量参照文献[22]方法测定，采用 Braford 法测定可溶性蛋白质，各物质含量结果表示为 $mg{\cdot}g^{-1}$，还原糖含量表示为 $g{\cdot}L^{-1}$。

1.5 浆果代谢组的分析

每个试验点采用打孔器收集葡萄浆果的果肉、果皮和种子，混匀后取 100 mg 葡萄样品于 2 mL 离心管里，重复 3 次，萃取代谢物[26]，进行代谢组学分析[27]。

1.6 数据分析

采用方差分析法分析‘美乐’葡萄浆果不同品质指标在高海拔和低海拔区域的差异，利用最小二乘法判别分析法(PLS-DA)分析高海拔和低海拔区域葡萄品质差异分布。选取 2013 年和 2014 年葡萄从萌发到收获的气象数据，统计平均温差、最大温差、日均温度、生长时期有效积温、日均相对湿度、降雨量、日均日照时长、日均光辐射强度、总光辐射强度、日均紫外辐射强度、总紫外辐射强度。利用整合通路分析(IPA)分析高海拔和低海拔区域浆果代谢通路的差异，利用代谢物组富集分析(MEPA)分析高海拔和低海拔区域对浆果代谢通路的富集[23–25]。采用 Concoco 5.0 软件中的去趋势化对应分析(DCCA)分析高海拔和低海拔区域的品质因子和差异代谢物的含量与气象因子的关联关系。

2 分析与结果

2.1 不同海拔‘美乐’葡萄产区的气象特征

由表 2 可知，高海拔区域的葡萄园日均温差、生长时期有效积温、降雨量、日照辐射和紫外辐射高于低海拔区，相对湿度、日均温、氧气含量高海拔区域的葡萄园数值低于低海拔区。

表 2 不同海拔‘美乐’葡萄产区的气象因子
Table 2 Climate parameters of ‘Merlot’ wine-producing areas at different altitudes

气象因子 Climatic factor	海拔 Altitude (m) 41	2 343
日均温差 Average daily temperature difference (℃)	20.5	21.3
日均温度 Average daily temperature (℃)	20.3	20
生育期有效积温 Effective accumulated temperature during growing period (℃)	1 425.7	1 691.9
日均湿度 Average daily humidity (%)	70.9	55.7
生育期降雨量 Rainfall during growing period (mm)	144	369
年日照时数 Annual sunshine duration (h)	2 193.5	2 688.0
日均日照时数 Average daily sunshine duration (h)	10.5	15.2
辐射 Radiation ($W{\cdot}m^{-2}$)	14 497	15 751
日均辐射 Average daily radiation ($W{\cdot}m^{-2}$)	125.6	157.1
日均紫外辐射 Average daily UV radiation ($W{\cdot}m^{-2}$)	2.4	3.8
紫外辐射 UV radiation ($W{\cdot}m^{-2}$)	256.5	674.2
空气氧气含量 O_2 content of air (%)	20.94	20.20

2.2 不同海拔区‘美乐’葡萄浆果的品质和代谢物特征

高海拔区葡萄园的‘美乐’葡萄浆果总酚、可溶性固形物含量显著高于低海拔区葡萄园，花青素、单宁含量显著低于低海拔葡萄园，还原糖、蛋白质、酒石酸、黄酮和类黄酮含量及 pH 无显著差异(表 3)。

表 3 不同海拔‘美乐’葡萄产区葡萄品质的比较
Table 3 ‘Merlot’ berries compositions in wine-producing areas at different altitudes

内含物 Composition	海拔 Altitude (m) 41	2 343	*P*
总酚 Phenol ($mg{\cdot}g^{-1}$)	4.54	8.31	0.000**
花青素 Anthocyanins ($mg{\cdot}g^{-1}$)	1.37	0.96	0.001**
单宁 Tanins ($mg{\cdot}g^{-1}$)	7.81	3.73	0.003**
可溶性固物 Soluble solid content (%)	17.50	25.18	0.005**
类黄酮 Flavonaid ($mg{\cdot}g^{-1}$)	9.53	7.62	0.058
还原糖 Reducing sugar ($g{\cdot}L^{-1}$)	276.85	319.01	0.150
蛋白质 Protein ($mg{\cdot}g^{-1}$)	1.01	1.40	0.451
总酸 Total acid ($g{\cdot}L^{-1}$)	8.64	7.63	0.471
pH	4.03	4.30	0.505
黄酮 Flavone ($mg{\cdot}g^{-1}$)	2.64	1.87	0.526

** 表示在 0.01 水平下显著相关。** means significant correlation at 0.01 level.

PLS-DA 分析表明, 高海拔与低海拔区'美乐'葡萄浆果品质差异极显著。从图 1A 可知, PC1、PC2 总和为 85.9%, 能代表所有的品质因子, 高海拔环境与 pH、总酸、单宁、总类黄酮、还原糖正相关, 与可溶性蛋白质、总酚、总黄酮、可溶性固形物、花青素负相关。PC1、PC2 能代表高海拔与低海拔差异对代谢物的影响(图 1B), α-麦胚酚、Maleamate、甘油、根皮素、橙皮素、刺芒柄花素、松柏醛、木糖醇、N-methly-glutamate、酒石酸、延胡索酸、胍基琥珀酸、甲基丙二酸、苏糖酸、甘油酸、半乳糖酸、莽草酸、亚油酸、油酸、Mesaconic、葡糖酸、、腐胺、黄苷、脯氨酸、脱氧鸟苷、5-甲氧色胺、N-甲酰-L-蛋氨酸、S-羧甲基半胱氨酸、甘氨酸、胸苷等代谢物含量与海拔梯度正相关; 肌醇、儿茶素、酵母甾醇、甘露醇、乙醇酸、琥珀酸酯、二氨基庚二酸、硬脂酸、甘露糖、核糖、核糖醇、乳糖、白藜芦醇等代谢物含量与海拔梯度负相关。

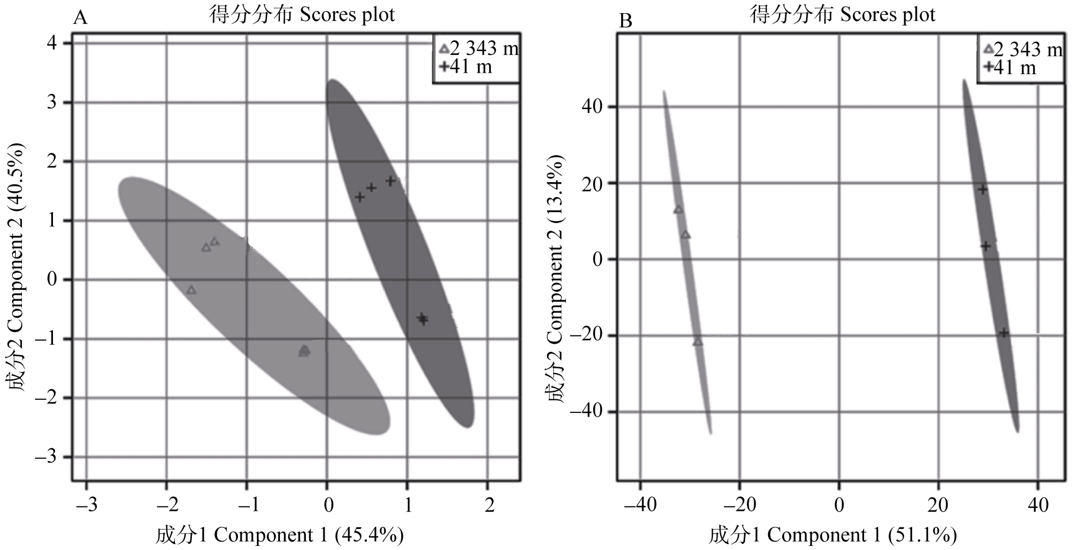

图 1　不同海拔'美乐'葡萄产区葡萄品质指标**(A)**和代谢物种类和含量**(B)PLS-DA** 分析结果图

Fig. 1　PLS-DA analysis of quality indexes (A) and metabolite profiles of 'Merlot' berries in wine-producing areas at different altitudes

2.3　不同海拔区'美乐'葡萄浆果的代谢物通路

氨基酸是葡萄浆果中的重要物质。不同海拔区'美乐'葡萄浆果的氨基酸代谢通路(图 2)显示, 高海拔环境增强葡萄浆果的丝氨酸到甘氨酸和半胱氨酰甘氨酸通路, 丙酮酸盐到 5-甲氧色胺通路, 丙酮酸到 D-丙氨酰丙氨酸代谢, TCA 循环中的草酰乙酸到 N-甲酰-L-蛋氨酸代谢, TCA 循环中 2-酮戊二酸到腐胺代谢, 2-酮戊二酸到脯氨酸代谢, 鸟嘌呤到脱氧鸟苷代谢, 尿酸到胸苷代谢, 肌苷酸到黄苷代谢。

有机酸是葡萄浆果中的重要物质。不同海拔区'美乐'葡萄浆果的有机酸代谢通路(图 3)显示, 与低海拔环境相比, 高海拔环境增强葡萄浆果甘油到苏糖酸、丙酮酸盐到莽草酸、乙酰 CoA 到亚油酸、乙酰 CoA 到油酸、柠檬酸盐到甲基丙二酸、琥珀酸到胍基琥珀酸和酒石酸、TCA 循环中的柠檬酸盐到葡糖酸和尿刊酸、半乳糖醇到半乳糖酸代谢; 减弱延胡索酸到琥珀酸、柠檬酸盐到二氨基庚二酸、丙酮酸盐到甘油酸、乙酰 CoA 到硬脂酸、乙酰 CoA 到丙二酸的代谢。

高级醇和酚类物质是葡萄浆果中的重要物质。不同海拔区'美乐'葡萄浆果的高级醇及酚类物质代谢通路(图 4)显示, 与低海拔环境相比, 高海拔环境增强葡萄果实浆果甘油醛到甘油、甘露醇、松脂醇到松柏醛、色氨酸到 α-麦胚酚、葡萄糖到 N-methly-glutamate、葡萄糖到 meleamate、丙二酰 CoA 到根皮素、葡萄糖醇到木糖醇、葡萄糖苷到橙皮素和刺芒柄花素代谢; 减弱葡萄糖到核糖醇、丙二酰 CoA 到儿茶素和白藜芦醇、5-燕麦甾-烯醇到酵母甾醇、葡萄糖到到甘露醇的代谢。

糖类是葡萄浆果中的重要物质。不同海拔区'美乐'葡萄浆果的糖类代谢通路(图 5)显示, 与低海拔环境相比, 高海拔环境增强葡萄果实浆果的 1-4β 半乳糖甙–果糖代谢, 降低 D-葡萄糖到核糖、Epimelibiose 到甘露糖和半乳糖的代谢。

2.4　不同海拔区'美乐'葡萄浆果代谢物的通路富集

从图 6 可知, 不同海拔区'美乐'葡萄浆果代谢物的通路富集发现 8 条氨基酸代谢、4 条碳水化合物代谢、3 条脂质代谢、3 条氮代谢。氨基酸代谢是氨

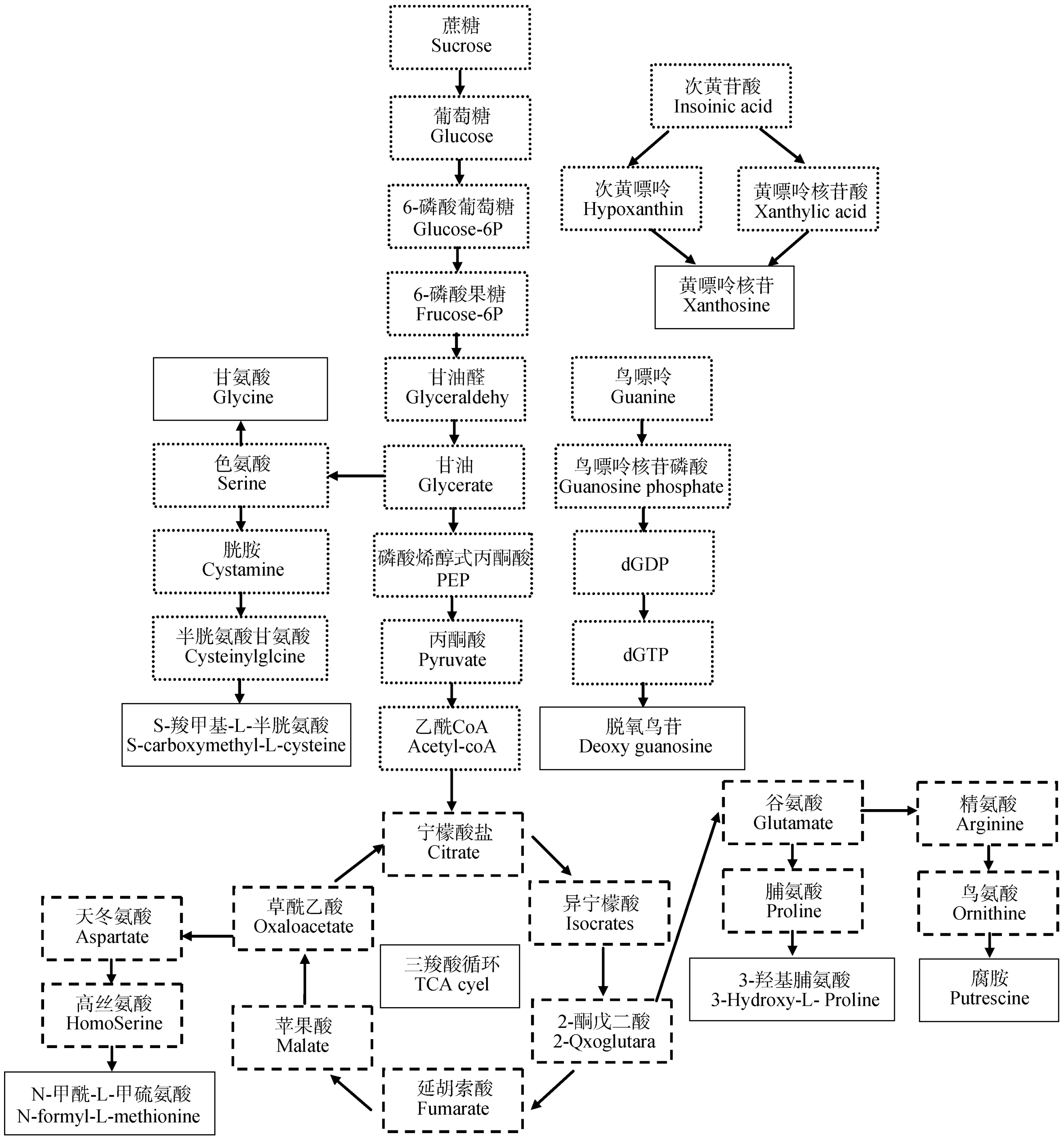

图 2　不同海拔区'美乐'葡萄浆果的氨基酸类代谢通路图

Fig. 2　Amino acid metabolome pathways for 'Merlot' grape berries in wine-producing areas at different altitudes

实线边框表示高海拔代谢物含量显著高于低海拔(P<0.05)，点虚线边框表示代谢物含量在高海拔与低海拔间无显著差异(P>0.05)，短划线边框表示高海拔代谢物显著低于低海拔代谢物(P<0.05)。下同。Solid line boxes show significantly higher metabolites contents at high altitude region than at low altitude region (P < 0.05). Dotted line boxes show no significant difference in metabolites between high and low altitude regions (P > 0.05). Dashed line boxes show significant lower metabolites contents at high altitude region than at low altitude (P < 0.05). The same below.

基酸生物合成、降解、蛋白质生物合成的重要通路。本研究中，高海拔区域'美乐'葡萄浆果增强缬氨酸、亮氨酸和异亮氨酸的生物合成代谢，甘氨酸、丝氨酸和苏氨酸代谢。本研究中高海拔区域增强'美乐'浆果中的半乳糖代谢、果糖和甘露糖代谢，减弱淀粉和蔗糖代谢，增强饱和脂肪酸和甘油酯的生物合成代谢，减弱类固醇的生物合成代谢、萜类化合物骨架生物合成代谢，增强嘧啶代谢、氨基糖和核苷酸糖代谢(图 6)。

2.5　环境气象因子与'美乐'葡萄浆果代谢物的关系

采用 Concoco 5.0 软件中的 DCCA 方法分析低海拔和高海拔产区气象因子与代谢物的关系(图 7)发现：低海拔和高海拔产区气象因子中的日均时长、生长时期总辐射、日均辐射、温差、日均温度、生长时期有效积温与'美乐'浆果内含物含量密切相关，与高海拔环境减弱代谢物和高海拔环境增强代

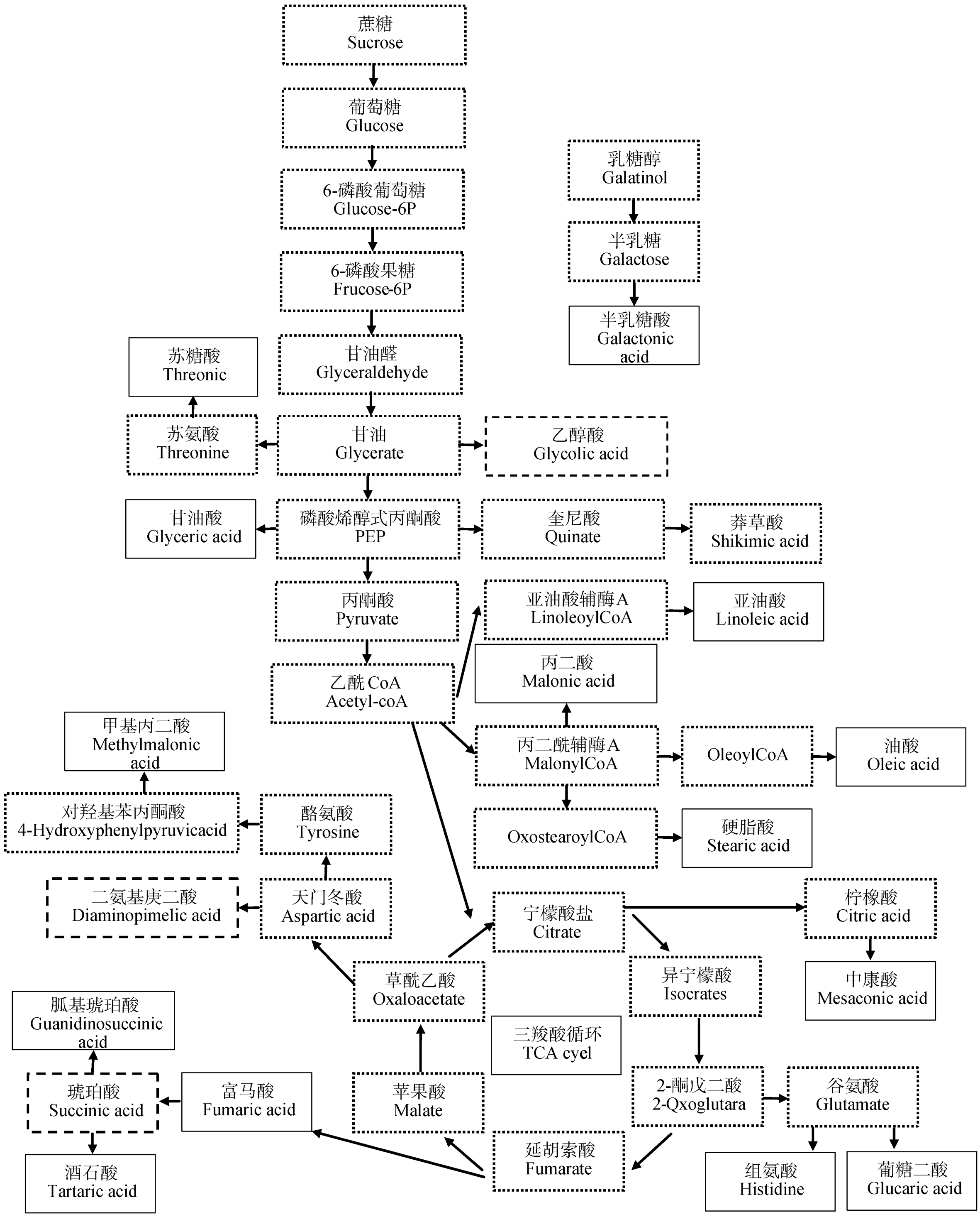

图 3　不同海拔区‘美乐’葡萄浆果的有机酸类代谢通路图

Fig. 3　Organic acid metabolome pathways for ‘Merlot’ grape berries in wine-producing areas at different altitudes

谢物密切相关，其他因子如空气中的氧气含量、降雨量、湿度、生长时期日照时长、紫外辐射与‘美乐’浆果内含物含量、高海拔环境减弱代谢物和高海拔环境增强代谢物相关性弱。因此，可以推断低海拔和高海拔产区导致‘美乐’浆果代谢物差异的主要气象因子是日均时长、生长时期总辐射、日均辐射、温差、日均温度和生长时期有效积温。

3　讨论

本研究中高海拔区‘美乐’葡萄浆果能正常成熟，且品质优于低海拔区域。高海拔产区与低海拔产区相比增加多种代谢物的含量，降低多种代谢物含量。过去的研究认为高海拔区域限制葡萄产量、葡萄品质和葡萄酒品质，如海拔梯度增加会降低葡萄

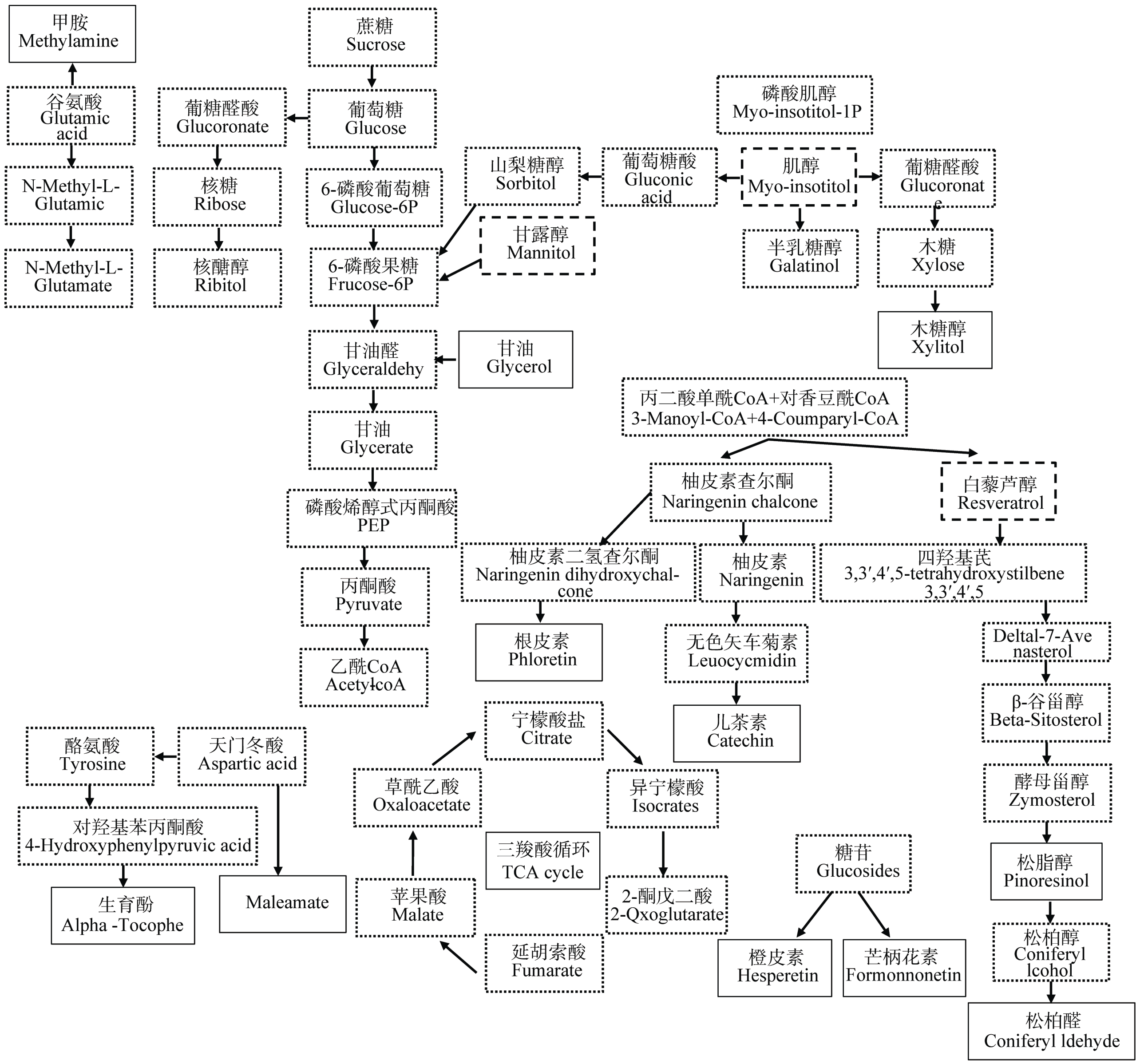

图 4 不同海拔区‘美乐’葡萄浆果的醇类和酚类代谢通路图

Fig. 4 Alcohols and phenols metabolome pathways for ‘Merlot’ grape berries in wine-producing areas at different altitudes

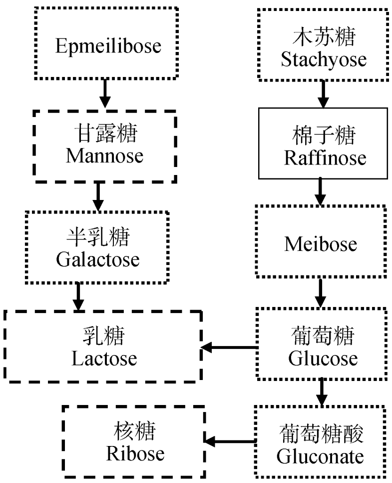

图 5 不同海拔区‘美乐’葡萄浆果的糖类代谢通路图

Fig. 5 Sugars metabolome pathways for ‘Merlot’ grape berries in wine-producing areas at different altitudes

浆果的可溶性固形物和花色素含量、升高酒石酸含量等[28]。本研究证明在更高海拔的产区,‘美乐’葡萄浆果仍获得较高的品质,海拔 2 343 m 区域适合生产高品质的‘美乐’葡萄。

代谢通路分析和富集发现,高海拔产区与低海拔产区相比增强‘美乐’葡萄浆果多条氨基酸、核酸、黄苷、有机酸、甘油醛、甘露醇、松柏醛、α-麦胚酚、N-methly-glutamate、meleamate、根皮素、木糖醇、橙皮素和刺芒柄花素代谢、1-4β 半乳糖甙-果糖代谢;降低核糖、半乳糖、琥珀酸、二氨基庚二酸、甘油酸、硬脂酸、丙二酸、核糖醇、儿茶素、白藜芦醇、酵母甾醇代谢。研究认为氨基酸参与葡萄多种生理功能,如调控浆果后熟过程和非生物逆境的抗性[16,29−32],高海拔环境能加速‘美乐’葡萄浆果

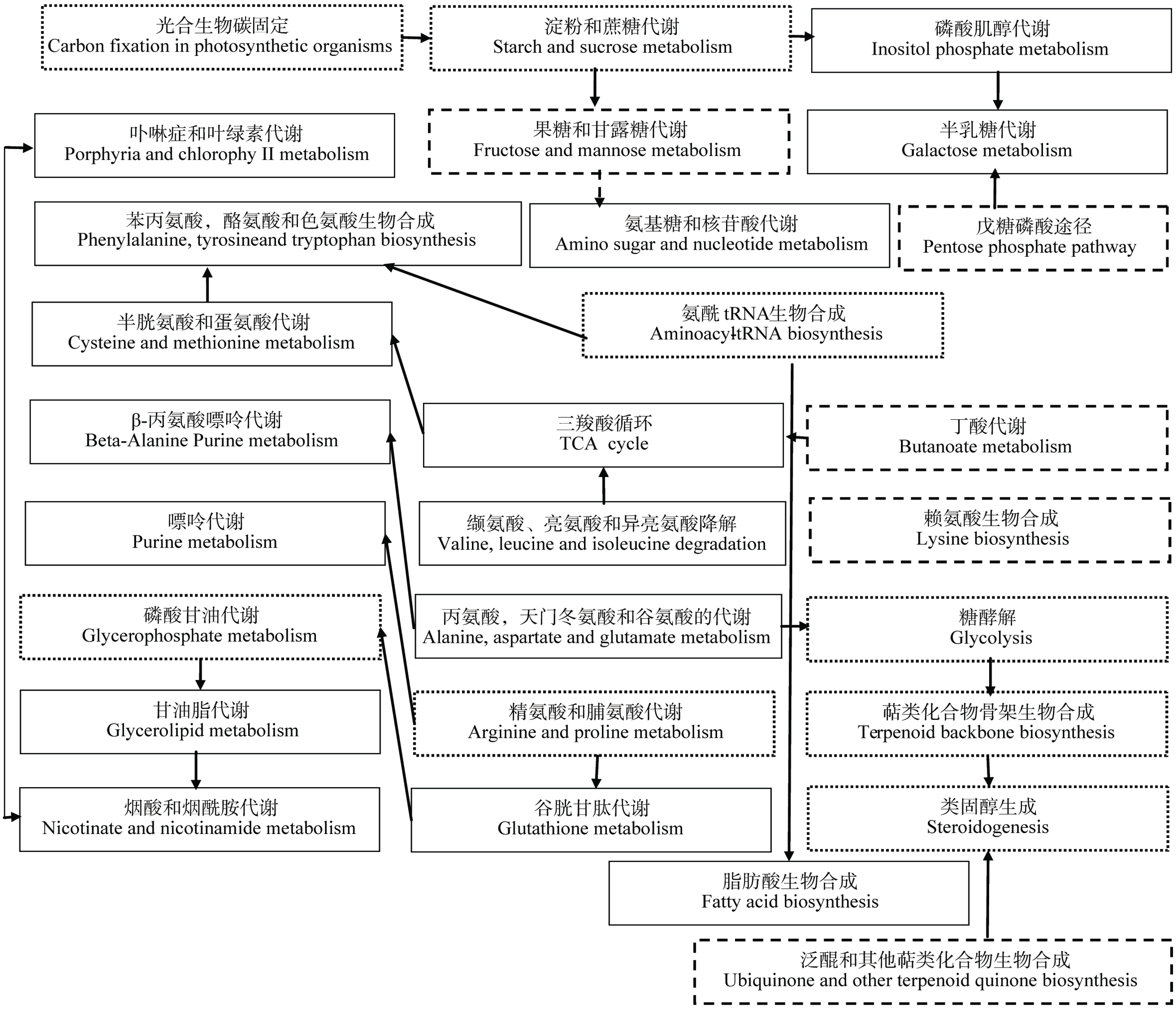

图 6　不同海拔区‘美乐’葡萄浆果代谢通路富集图

Fig. 6　Metabolome pathway enrichment for ‘Merlot’ grape berries in wine-producing areas at different altitudes

成熟和调控采后生理，利于浆果的储存和延迟采收，增强抗性和适应气象变化，核酸代谢、黄苷代谢在葡萄代谢中鲜有报道，参与葡萄的何种生物学功能还未完全清楚[30−31,33−40]，高海拔环境利于提高‘美乐’葡萄浆果的品质和潜在葡萄酒的风格和品质；有机酸调控单宁的浓缩度和脂肪代谢，调节渗透压和葡萄的成熟度以及酒的口感、影响葡萄酒的风格和品质，参与抗氧化活力、抗癌活性、抗凋亡等生物学功能，调控动物免疫反应等功能[7,11,15,37,29−36]，高海拔环境更利于提高葡萄品质和代谢物的生物学活性；高级醇和酚类物质与葡萄酒的口感、抗真菌侵染、抗非生物逆境、抗癌活性有关[41−46]，高海拔环境增强葡萄的口感、抗逆性、提高氧气利用率、保健防病价值；研究认为糖类参与多种生物学功能，如类黄酮和白芦藜醇的合成、调控黄酮通路、参与细胞壁、糖和酒石酸的生物合成、提供营养纤维[5,47−48]，高海拔环境增强葡萄的相关代谢，提高葡萄的品质。

过去研究认为代谢物通过对代谢网络的反馈调节和负反馈调节实现代谢物的生物学功能[24]。本研究证明高海拔环境增强了‘美乐’葡萄浆果通过调整代谢物的通路实现品质因子的积累和对物理环境的适应性，高海拔和低海拔环境条件下代谢物通路的差异是导致品质差异和风味差异的根本原因，高海拔和低海拔环境下大多数代谢物的通路是增强的。因此，高海拔环境‘美乐’葡萄浆果品质风味物质积累高于低海拔区。

本研究中代谢通路富集发现，高海拔区域‘美乐’葡萄浆果改变氨基酸、碳水化合物和酯类代谢，减弱类固醇、萜类化合物骨架生物合成代谢和氮代谢，高海拔美乐产区浆果的大多数代谢通路增强，其中甘氨酸、丝氨酸和苏氨酸代谢、淀粉和蔗糖代谢、减弱类固醇的生物合成代谢和萜类化合物骨架生物合成代谢减弱。过去文献中报道了代谢通路富集方法在代谢组中的应用[23−25]，但是在环境对酿

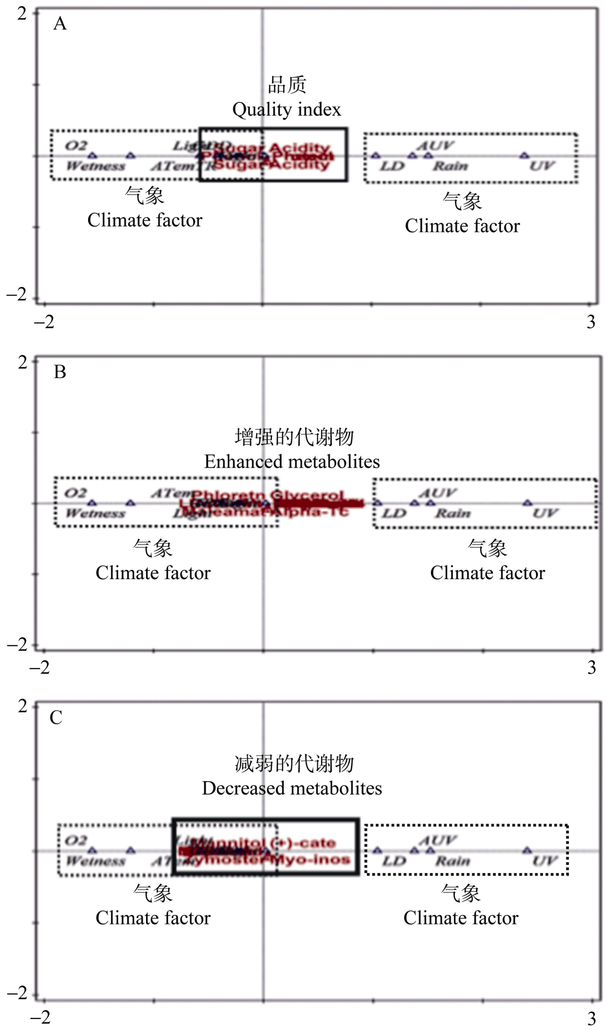

图 7　不同海拔区气象因子和‘美乐’葡萄浆果内含物和代谢物 **DCCA** 分析图

Fig. 7　DCCA analysis ‘Merlot’ grape berries compositions and metabolome with climate factors in wine-producing areas at different altitudes

A 是环境气象参数与浆果品质的关系, B 是环境气象参数与高海拔环境减弱代谢物的关系, C 是环境气象参数与高海拔环境增强代谢物的关系。图中实线框内为代谢物和品质因子, 虚线框内为气象因子。Figure A shows correlation between meteorological factors and fruit quality indexes. Figure B shows correlation between meteorological factors and weakened metabolites at high altitude region. Figure C shows correlation between meteorological factors and strengthened metabolites contents at high altitude region. In the figures, items in the solid-line boxes are metabolites and quality factors, those in the dash-line boxes are meteorological factors.

酒葡萄的影响研究中应用较少。本研究发现采用代谢通路富集方法更容易了解海拔高度对葡萄浆果代谢的影响, 从中可挖掘重要的差异代谢通路, 对了解高海拔产区酿酒葡萄的品质成因有重要的指导意义。

本研究中日均时长、生长时期总辐射、日均辐射、温差、日均温度、生长时期有效积温是调控‘美乐’浆果品质因子和代谢物的主要驱动力, 证实了过去研究的观点, 葡萄园的风土条件是影响葡萄品质的重要因子[29], 如日照时长、温差大小、紫外辐射等因子影响浆果品质[9,15,30–41]。与其他研究不同的是, 此研究中采用目前最有效的工具去趋势化对应分析方法把葡萄园的气象因子和浆果品质因子和代谢物进行关联分析, 证实前人研究的可靠性。

海拔为 2 343 m 的葡萄园的气象因子是‘美乐’葡萄浆果品质因子优于低海拔产区的主要原因, 气象因子通过驱动浆果物代谢通路的多样性来实现氨基酸、有机酸、醇、多酚和糖类的积累, 高海拔‘美乐’葡萄浆果积累更多的氨基酸、有机酸、醇、多酚、糖类, 这些代谢物通过代谢网络的反馈调节和负反馈调节调整三羧酸循环的产物和糖、核酸、黄苷、酚代谢来适应高海拔逆境, 提高品质。

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